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Distinct locomotor control and awareness in awake sleepwalkers

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eTOC Blurb: *Sleepwalking is a common parasomnia permitting complex actions to occur outside of consciousness. Kannape et al. show that, also in awake behaviour, sleepwalkers have a different level of conscious awareness when walking under cognitive load, mimicking nocturnal sleepwalking episodes.*

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Sleepwalkers' (SW) complex nocturnal behaviors have inspired fictional characters from Shakespeare's Lady Macbeth to Polidori's Vampyre to Cesare, the homicidal somnambulist in *The Cabinet of Dr Caligari*. Yet although the underlying pathophysiology of sleepwalking, i.e. the partial arousal from slow-wave sleep, is today well-documented, the detailed sensorimotor mechanisms permitting locomotion and further complex behaviors to occur outside of conscious control remain poorly understood [1]. Further, the paroxysmal character, nocturnal pattern, and spontaneous onset have made it nigh impossible to study somnambulism behaviorally during wakefulness. The novel goal-directed walking paradigm reported here, based on full-body motion capture and virtual reality feedback, directly addresses this issue and provides unique insights into the functional mechanisms of this common parasomnia: SW exhibited improved movement automation and a stronger dissociation between locomotor control and awareness than matched controls when challenged with a cognitive load. Our data therefore suggest that behavioral markers exist in awake SW, characterized by their ability to perform complex locomotor actions in the absence of full consciousness. Our findings are important as they firmly link sleepwalking to the neuroscience of motor control and motor awareness and may complement formal diagnosis procedures (normally requiring time- and cost intensive sleep studies and polysomnographic recordings).

Dissociations between automated motor control and awareness, so striking in each sleepwalking episode, have been extensively studied in healthy populations, albeit at much weaker dissociation levels [2]. Generally inspired by the comparator framework [3], such paradigms quantify participants' motor awareness and performance when exposed to different spatiotemporal mismatches concerning auditory or visual feedback about on-going

movements [4,5]. Such paradigms have recently been adapted to locomotion, and in combination with dual tasking [6] have illustrated an increased dissociation between locomotor control and awareness under cognitive load [7,8].

To investigate both locomotor control and awareness in SW, we asked a group of clinically diagnosed SW and a group of age- and gender-matched control participants to move their tracked, virtual body into a virtual target cylinder by performing the corresponding goal-directed movement in the tracking arena (Figure 1A, see Supplemental Experimental Procedures). Feedback of walking trajectories could be veridical or randomly deviated to the left/right by 5°-30° such that participants had to compensate for the deviation in order to reach the target [8]. Participants rated the veracity of the received feedback after each trial (yes/no response; one block as described; one block in dual task condition; counterbalanced). The secondary task was articulated backwards counting (steps of 7), a task reliably shown to interfere with locomotor control (independent of errors in arithmetic) [6].

All participants correctly performed the task and accurately identified that the virtual body reflected their own movements in control trials ($93 \pm 2\%$ $\mu \pm \text{SEM}$ self-attribution, cf. Table S1) and correctly rejected strongly deviated trials ($4 \pm 2\%$ self-attribution for 30° mismatch, main effect of Deviation: $P < 0.001$), closely replicating previous results [7,8] (Bayes factor analysis $\text{BF} = 4.58$, half-normal prior derived from [8]). As illustrated in Figure 1D, there were no overt differences in locomotor awareness thresholds (Controls: $13.4^\circ \pm 1.5$, SW: $13.2^\circ \pm 1.7$) or walking performance (accuracy, velocity) between the groups in the single task condition.

However, under cognitive load, our study reveals two key findings that link sleepwalking to motor control and motor awareness in wakefulness. The first important finding is the SW's ability to maintain the sequential locomotor pattern under cognitive load. Whereas, walking velocity was significantly affected by cognitive loading overall ($.70 \pm .15\text{m/s}$ to $.65 \pm .14\text{m/s}$, $P=.010$), there was an interaction between factors Group and Task ($P=.014$). In-line with clinical locomotion data, control participants significantly slowed down when performing the secondary task ($.68 \pm .20\text{m/s}$ to $.59 \pm .18\text{m/s}$, $P<.001$) whereas SW maintained similar walking velocities across conditions ($.73 \pm .22\text{m/s}$ to $.72 \pm .21\text{m/s}$, $P=.59$, Figure 1C). This suggests that the degree of walking automaticity in the present SW differs from controls, as hypothesized (cf. Supplemental Experimental Procedures).

The second key finding is that SW correctly rejected significantly more deviated trials under cognitive load than control participants. This is reflected in the opposing effects dual tasking had on the two cohorts: 50% awareness thresholds decreased to $10.5^\circ \pm 1.0$ for SW whereas thresholds increased to $16.5^\circ \pm 2.3$ in the control group, in-line with previous results in healthy participants [7,8] (significant interaction Group by Task: $P=.016$; interaction $BF=15.70$ using normal prior based on control participant data). We note that this change in SW locomotor awareness thresholds is unlike previous control [8] or patient groups (such as persons with schizophrenia or de-afferented neurological patients) who tend to overly rate action-feedback as self-generated, particularly in trials with high ambiguity or uncertainty. Such attribution errors have been described as arising from sensory noise or, in the case of participants diagnosed with schizophrenia, impairments in the underlying comparator mechanism [9]. However, SW showed the opposite response pattern and correctly rejected deviated feedback trials under cognitive load. These differences are also not explained by a

difference in motor compensation (see Figure 1B for example paths), as walking accuracy, measured at the trajectory endpoint, did not statistically differ significantly across the single and dual task conditions ($P>0.20$). There was further no significant correlation between the walking velocity and the awareness thresholds (neither in the single-, dual-task condition, nor the aggregate, all $P>0.07$), indicating that the locomotor awareness differences observed in the dual task condition are due to our experimental manipulation and not a change in walking characteristics.

Novel behavioral paradigms such as the one proposed here are required to improve neuroscientific understanding and potentially complement diagnostics in somnambulism (cf. binary logistic regression in SI) [1]. Although the present data should be regarded with caution (sample size; single-blind design), we argue that the experimentally-induced wakeful locomotor state in the present SW cohort bears resemblance to their nightly walking episodes in the absence of full consciousness. Our findings link SW to the neuroscience of locomotor control and awareness and characterise a potential behavioural marker of SW during full wakefulness that only becomes overt while walking under cognitive load. Further investigating awareness for upper-limb movements and other aspects of motor control (such as motor preparation and planning) [10] may help establish whether the alteration of motor control and awareness in SW is specific to locomotion or whether it impacts sensorimotor control more generally. Finally, the “ambulatory” paradigm presented here may contribute to improving reliability and economization of SW diagnosis by applying the principles of human neuroscience to the investigation of these nocturnal behaviors historically shrouded in myth.

AUTHOR CONTRIBUTIONS

Conceptualization O.A.K. and O.B.; Methodology O.A.K. and O.B.; Investigation O.A.K. and O.B.; Formal Analysis O.A.K. and O.B.; Resources A.O.R. and S.P.; Writing – Original Draft O.A.K. and O.B.; Writing – Review & Editing O.A.K., O.B., A.O.R., and S.P.; Visualization O.A.K.; A.O.R. and S.P. provided expertise and feedback.

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FIGURES & LEGENDS

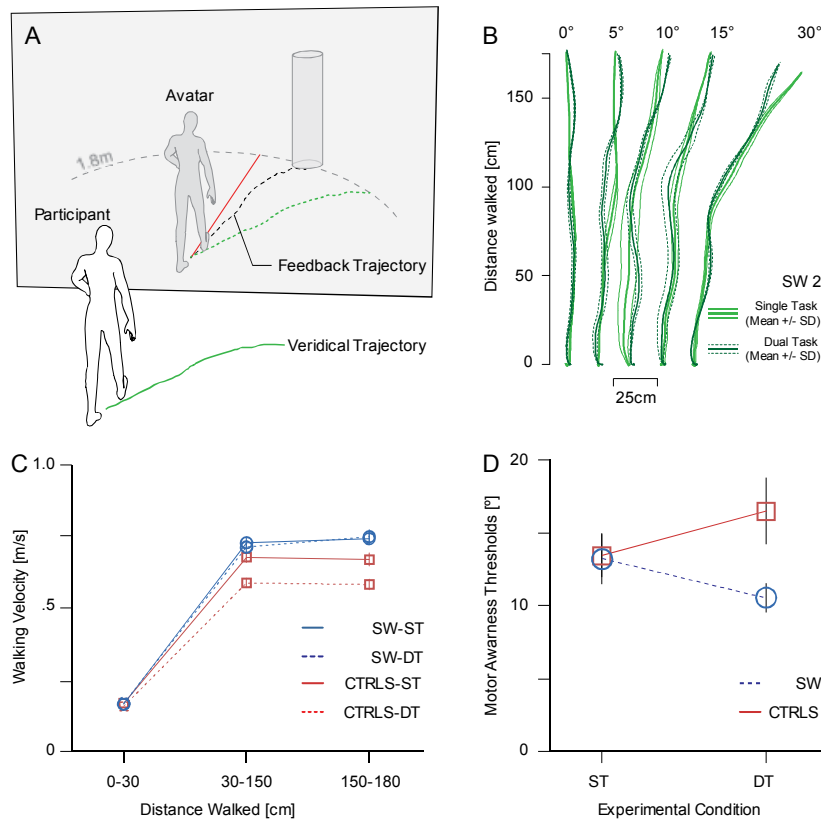
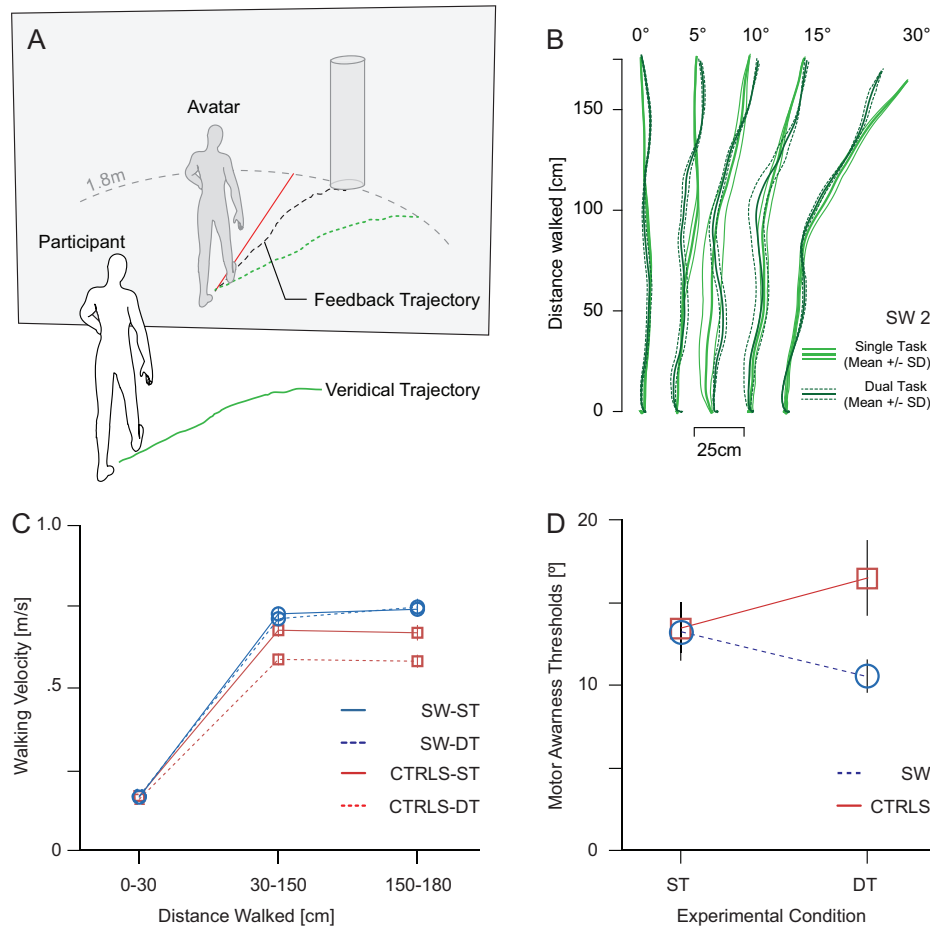


Figure 1 – A) Participants performed a goal-directed walking task in a Virtual Reality environment. They received life-size visual feedback of their movements on a rear-projection screen using full body motion capture. While walking towards one of four randomized target-locations, feedback could be veridical or deviated to the left or right by 5° to 30° (solid red line). Participants compensated for this deviation in order to reach the target (dotted green line). B) All participants correctly compensated for the introduced angular deviations to reach the virtual target location (left/right collapsed). Motor compensation as measured at the trajectory endpoint was not significantly affected by cognitive loading and did not differ between sleepwalkers and control participants. Overall participants compensated for $56 \pm 4\%$ ($\mu \pm \text{SEM}$) of the introduced deviation in the single task and $60 \pm 4\%$ in

the dual task condition. C) Walking velocities were calculated for the initial step (0-30cm), the main trajectory (30-150cm), and the final step (150-180cm) to remove initial freezing or hesitation at the end of the trial. As indicated in the figure, control participants significantly slowed down under cognitive loading, whereas SW maintained their walking velocity in both conditions. D) At the end of each trial participants judged whether or not the movement shown on the screen corresponded to the movement they had just performed. These ratings were used to generate 50% motor awareness thresholds. Sleepwalkers' and control participants' awareness thresholds largely overlapped in the single task (ST) condition but were differently affected by cognitive loading (dual task, DT). While control participants over-attributed more deviated feedback trials in the dual task condition, leading to higher awareness thresholds (solid red line), SW correctly rejected more of these trials under cognitive load (dotted blue line).

Figure



Supplemental Information: Distinct Locomotor Control and Awareness in Awake

Sleepwalkers

Oliver A Kannape, Stephen Perrig, Andrea O Rossetti, Olaf Blanke

Supplemental Data

Table S1 – Related to main results. Motor Awareness (MA) and Motor Performance (MP) as a function of introduced angular mismatch in the Single (ST) and Dual Task (DT) conditions. MA reflects the percentage of trials perceived not to match participants' own movements. SW = sleepwalkers; CTRL = control participants

		ST ($\mu \pm \text{SEM}$)					DT				
		0°	5°	10°	15°	30°	0°	5°	10°	15°	30°
MA	SW	7.40	15.83	36.64	62.00	94.89	16.34	22.01	47.25	67.65	97.27
		± 2.80	± 5.28	± 7.74	± 7.28	± 3.66	± 5.15	± 4.81	± 6.84	± 5.63	± 1.61
	CTRL	6.27	10.55	34.14	61.05	97.04	6.18	16.69	29.50	53.02	84.37
		± 2.81	± 4.86	± 7.78	± 8.72	± 1.33	± 1.74	± 4.76	± 8.38	± 9.96	± 7.00
MP	SW	0.74	3.24	5.24	8.46	12.74	0.96	3.91	6.02	7.78	13.04
		± 0.18	± 0.29	± 0.33	± 1.12	± 1.76	± 0.21	± 0.25	± 0.55	± 0.61	± 1.57
	CTRL	0.86	3.80	5.76	8.42	13.45	1.12	3.99	6.28	8.58	15.01
		± 0.17	± 0.42	± 0.34	± 0.76	± 1.44	± 0.23	± 0.17	± 0.32	± 0.51	± 1.55

Supplemental Experimental Procedures

Participants

In total N=11 sleepwalkers (7 males, age $\mu=26 \pm 13$ years) and eleven age and gender-matched control participants took part in the study. All sleepwalkers (SW) had previously been diagnosed by neurologists and certified sleep specialists, co-authors AOR and SP, based on clinical criteria according to the International Classification of Sleep Disorders. The SW were approached by their corresponding, attending physician and voluntarily participated in the study. The single-blind study was approved by the local ethics committee (University Hospital Lausanne, Switzerland).

Materials

The materials and the experimental procedure match the protocol used in [S1]. Participants' movements were tracked and recorded using an active optical motion capture system (20 IR markers, ReActor2, Ascension Technology Corp., Burlington, VT, USA) at a sampling rate of 30 Hz. One marker each was placed on the sternoclavicular joint and the lower sternum, bilaterally on heel, lateral knee and elbow, dorsal hand and acromioclavicular (AC) joint, four markers on left-right, anterior-posterior superior iliac spine (SIS) and four on

the head. Walking trajectories were determined by the average SIS marker position. A schematic of the setup and task is illustrated in Figure 1A, main article. Participants received visual feedback of their movements by way of a 3.20m by 2.35m back-projection screen (width by height, 1280 x 1024 pixels, 60 Hz), with the screen itself forming part of the back-wall of the 4.11m by 4.11m tracking arena (projector: JVC DLA-SX21 projector, JVC U.S.A., Wayne, NJ, USA). In all trials, participants viewed an individually mapped, life-size virtual body perform their movements in real-time (intrinsic system delay of 75ms) using Autodesk MotionBuilder software (Autodesk Inc., San Rafael, CA, USA).

Experimental Procedure

The experimental procedure is illustrated in Figure 1A. Each trial started from a predefined location in the motion capture area. A semi-transparent target cylinder was shown in the virtual room at one of four randomized locations as shown on a rear-projection screen. Participants were asked to walk through the virtual target with their virtual body by walking in the motion capture area. In some trials, in randomized order and beyond a distance of 30 cm from the start location, the walking trajectory of the virtual body was systematically deviated towards either the left or the right (by 5°, 10°, 15° or 30°). The deviation of the virtual trajectory was calculated relative to the straight line between the participants' current position and the position of deviation onset. Direction and amplitude were randomised on a trial-by-trial basis. A trial ended as soon as the participant reached the target distance of 180 cm, independent of reaching the centre of the target cylinder. Subsequently, participants indicated using a joystick whether the feedback shown on the screen corresponded to the movement they had just performed.

Participants performed two experimental blocks, a single task session (ST) and a dual task session (DT), counterbalanced across participants. Each block contained 88 trials, including 24 control trials, i.e. no deviation, and 16 trials per deviation, randomized but evenly distributed across direction and targets. In the DT block participants performed the same walking task while performing an articulated arithmetic task (serial-7 subtractions). Participants were instructed to continuously count and only stop while responding to the agency attribution question. They started counting from 200 and continued counting backwards throughout the entire block, ensuring that the cognitive load commenced before and lasted throughout each trial. We chose the serial-7 subtraction task, as it has been reported to cause gait changes such as a decrease in velocity in young healthy participants as well as patient populations.

Hypotheses

Given the complex behaviors performed during sleepwalking – with strongly impaired conscious access to involved sensorimotor and cognitive resources – we hypothesized that both locomotor control and awareness would differ from control participants, particularly when faced with an additional cognitive load. Gait-interference described in dual-task paradigms should be diminished in SW. In turn, the comparator mechanism underlying locomotor awareness should be less affected in SW, inhibiting the increase in awareness thresholds observed in non-SW participants under cognitive loading.

Dependent Variables

Motor Performance: Motor compensation was used to describe the total angle compensated by the participant taking into account the endpoint of each of their movement trajectories and measured from the onset of deviation at a distance of 30 cm to the start location. The mean position of the four hip markers was used to analyse all walking trajectories. Trials that were longer in duration than 10 seconds and trials that were corrupted through marker occlusions were omitted. All trajectories were interpolated over both time and space to 300 samples each. Furthermore, the trajectories were rotated from their four target locations at $\theta = (-30^\circ, -10^\circ, 10^\circ, 30^\circ)$ and overlapped onto a single target by transforming their samples into polar coordinates, rotating them, and returning them into the Cartesian coordinate format. Mean trajectories were obtained by taking the arithmetic mean of the x and z coordinates at each sample across all trials with the same angular deviation. The time and exact location of the participant at the press of the start button is used as the trial coordinate origin and start-time. Time to target is therefore the difference between the time-stamp of the first motion-capture sample that is further than 180 cm away from the start position and the trial start-time. The distance of the x-z location from this sample to the origin describes the exact distance the participant walked. The average walking velocity is determined by their ratio: distance over time in meters per second. Similarly, the velocities and durations for the start, middle, and end of the trial are calculated using the motion-capture coordinates and time-stamps as participants cross 30, 150, and 180cm.

Motor Awareness: MA was expressed by the number of no-responses out of all valid trials, grouped by angular deviation. Correct MA or self-attribution was a “yes” response for non-deviated, a “no” response for a deviated trial. Additionally, MA thresholds were determined psychometrically as described in the statistical analysis below.

Statistical Analysis

In the first instance a repeated measures ANOVA was conducted on factors Group (SW, Controls), Condition (ST, DT), and Deviation (0°, 5°, 10°, 15°, 30°) resulting in a 2 by 2 by 5 mixed design. Dependent variables were motor awareness and motor compensation (separate ANOVAs). A 2 by 2 ANOVA with factors Group and Condition was conducted for walking velocities, which were averaged across angular deviations, but split by start (0-30cm), middle (30-150cm), and end (150-180cm). ANOVAs and correlations were conducted in IBM SPSS Statistics [S2]. Motor awareness thresholds were extracted using the Psignifit toolbox [S3,S4] for Matlab [S5]. The thresholds reported here reflect the 50% point of subjective equality. Finally, Bayes Factorial (BF) analyses were conducted in R [S6] using the Bayes factor function from Kaye and Baguley [S7] based on Dienes [S8].

Supplemental Results

A binary logistic regression on the likelihood of participants being diagnosed sleepwalkers entering variables motor awareness, walking accuracy, and velocity (changes between DT and ST) yielded a significant model ($\chi^2(3) = 13.87, p = .003$) that correctly classified 10 out of 11 Sleepwalkers (91% correct) and 8 out of 11 controls (82% correct overall) with 62% of variance explained (Nagelkerke R^2). Change in MA was a significant factor (Wald=3.93, $p=.047$, Exp(B)=.613), with change in velocity at $p=.071$, and change in MP at $p=.375$.

Supplemental References

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